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Human-mediated dispersal in insects

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Central to the problem of biological invasions, human activities introduce species beyond their native ranges and participate in their subsequent spread. Understanding human-mediated dispersal is therefore crucial for both predicting and preventing invasions. Here, we show that decomposing human-mediated dispersal into three temporal phases: departure, transport and arrival, allows to understand how the characteristics of human activities and the biological traits of species influence each phase of the dispersal process, and ultimately govern invasion pathways in insects. Integrating these precise mechanisms into future invasion models should increase their realism and generalization for any potential insect invader. Moreover, understanding these mechanisms can provide insight into why some invasive insects are more widely distributed than others, and to estimate risks posed by species that have not yet been introduced.

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Introduction

All species are restricted in their geographical ranges. These limits are determined by the species' adaptations to the environment within their range, interspecific interactions and dispersal barriers [1]. Over the last few centuries however, humans have increasingly facilitated species' movements beyond their historical ranges [2,3] and the rate of new species introductions continues to rise due to the ongoing globalization of trade and travel [4,5]. Some introduced species are able to establish and become invasive, that is, they cause ecological or economic impacts in their introduced range [6]. These alien invasive species are the second most common cause of recent species extinctions, after biological resource usage [7]. In terrestrial ecosystems, insects are generally the most common and damaging group of animal invaders [8]. They cause a range of impacts on biodiversity, ecosystem services (such as nutrient cycling and carbon storage), or human and animal health, generating economic costs of at least 70 billion US$ annually [8,9]. Because of their small size, insects are easily transported by accident through human activities [10•]. In addition, they are sometimes introduced intentionally to serve as biological control agents, food or even as pets [11•].

Human-mediated dispersal is increasingly recognized as a key issue in invasion science [12,13••]. In numerous recent studies, genetic analyses have been used to reconstruct the global spread of many invasive insects [e.g. 14,15]. Most of these studies have found that individual histories of insect invasions tend to be complex and include frequent jump dispersal, multiple introduction events and back-introductions into native ranges [16]. Interestingly, introduced populations often become sources of new introductions via secondary introductions, a phenomenon termed the 'bridgehead effect' [15,17•,18]. This is a positive feed-back process whereby invasions generate new invasions and significantly contribute to rising invasion rates worldwide [19]. Yet, new invasions do not occur with equal probability across space and are linked to the intensity of human activities. It has been shown that countries with higher economic activity [20], population density [21] or human footprint [22] tend to receive a greater number of invasive species. However, proxies of human activities are typically general and have often been found to be poor predictors of new invasions [23]. Thorough knowledge of human-mediated transport is necessary to understand the precise mechanisms involved in the dispersal process and predict future invasion risk.

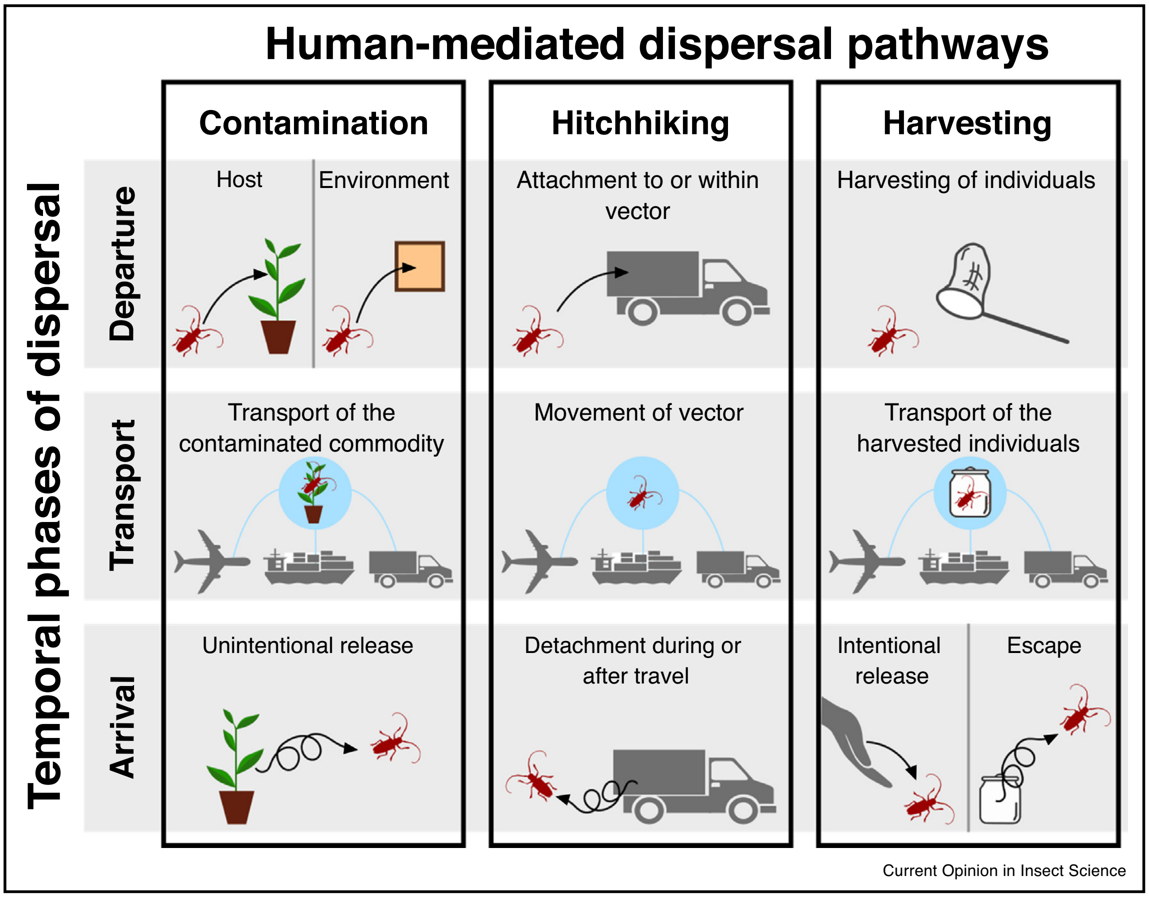
To achieve this, we propose distinguishing between three temporal phases in the human-mediated dispersal process (departure, transport and arrival), as these phases uniquely affect spread dynamics and the geography of invasions [13••,24]. Recognizing each of these phases is important for three reasons. First, it facilitates identifying the characteristics of different human activities that are key drivers of each dispersal phase. Second, it aids understanding of how human-mediated dispersal filters species based on their biological traits. Finally, it provides a basis for the prediction of invasion risk and the allocation of resources for managing the dispersal process.

Three phases in the human-mediated dispersal of insects

Like natural dispersal [25,26], human-mediated dispersal can be decomposed into three phases: departure, transport and arrival ([13••]; Figure 1). Departure covers the initiation of the dispersal process, for example, when a host substrate containing insects is loaded onto a transport vector, when insects attach to a potential transport vector or when insects are captured for shipping. Transport is the movement phase of the dispersal process; it can be performed by any type of vector, for example cars, trains, boats or airplanes. Arrival is the final phase of the dispersal process, when insects become disassociated with the transport vector, when they are released (intentionally or not), or when they escape captivity. Each phase is influenced by human activities that vary enormously in their frequency, spatial scale and direction.

The manner by which human activities drive the three phases of the dispersal process also depends on the pathway through which insects are dispersed [27]. The human activities dispersing insects can be classified into three types of pathways: contamination, hitchhiking and harvesting (Figure 1). The contamination pathway corresponds to the transportation of a commodity contaminated by insects (eggs, larvae or adults) either because the commodity is the insect's natural host (e.g. plants, mammals) or its immediate environment (e.g. soil, water) [10•]. For example, invasive fire ants (*Solenopsis invicta*) were shown to be dispersed during road maintenance by the transport of soil from invaded depots to maintenance sites (i.e. road shoulders) [28]. In the hitchhiking pathway, insects actively attach to an object not directly related to their natural environment (e.g. shipping container, car) [10•]. For instance, gypsy moths sometimes lay eggs on cars and trucks that are then transported while the vehicles travel, and the larvae eventually detach from these vectors after hatching [29]. The harvesting pathway consists of the intentional capture of insects by humans for some, often commercial, purpose (e.g. pet trade, biological control) [11•]. This last pathway

Figure 1



Decomposing human-mediated dispersal into three phases: departure, transport and arrival, for each invasion pathway. Contamination and hitchhiking pathways are accidental while in the harvesting pathway, species are intentionally captured and transported but arrival can be either intentional (release) or unintentional (escape).

leads to introductions either by intentional release or subsequent escape from captivity [2] (Figure 1). European bumblebees (*Bombus terrestris*) have been harvested and reared commercially for pollination purposes. They were directly released into the wild in New Zealand and escaped from glasshouses in Japan, two areas where they are now invasive [30].

Importantly, the characteristics of how humans travel or transport commodities (such as the distance travelled, the type and amount of transported commodities; Table 1) and the biological traits of species selectively transported by human-mediated dispersal (such as morphology, life histories or behavior; Table 2) depend both on the dispersal phase (i.e. departure, transport and arrival) and the dispersal pathway (i.e. contamination, hitchhiking or harvesting) [13••].

Characteristics of human activities

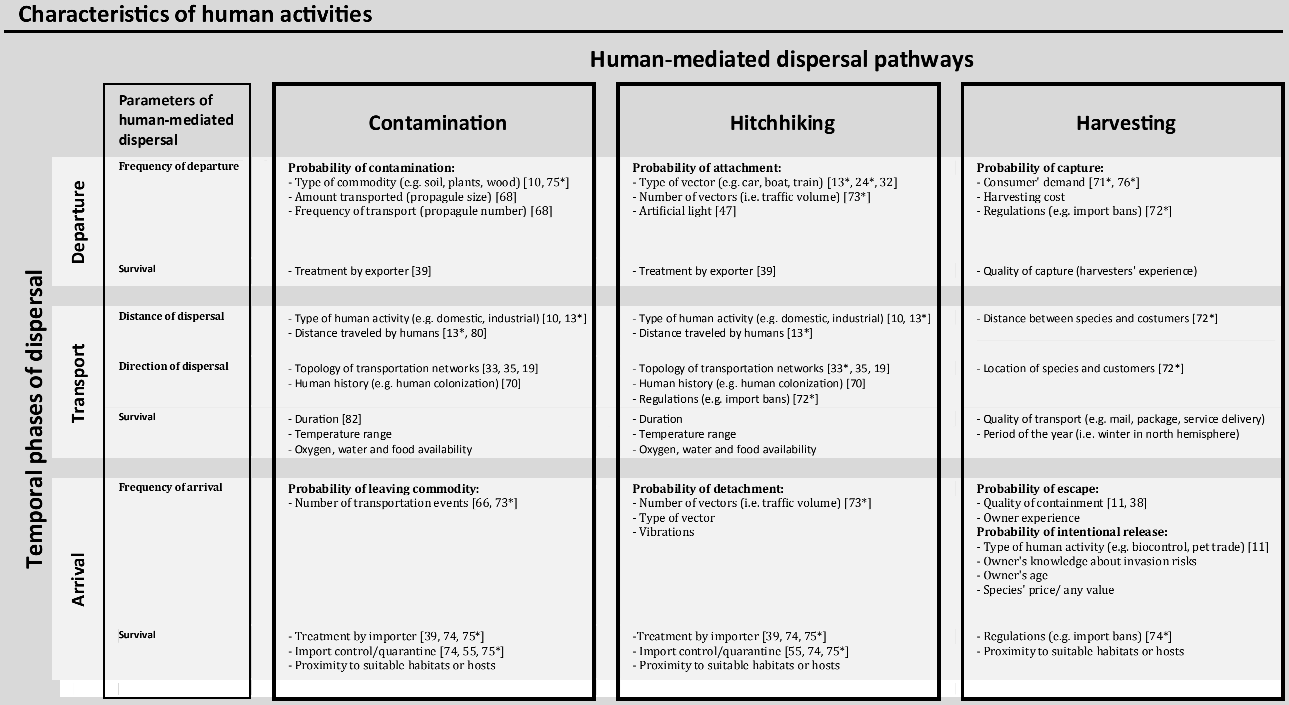
Departure phase. The key aspect of this dispersal phase is the number of individuals of a species that leave their native (or invasive) range. This population level of departure determines propagule pressure, a central feature of invasion success [31]. The quantity of transported commodities and traffic volume are important for the contamination and hitchhiking pathways, respectively, because they affect the frequency of dispersal events (propagule numbers), and the number of individuals transported per dispersal event (propagule size) [31,32•]. In the harvesting pathway, the frequency of departure typically depends on commercial factors such as costumers' demand or harvesting cost [11•].

Transport phase. The distance of human-mediated dispersal can vary strongly with different human activities. This is especially important for the contamination and harvesting pathways where species are less likely to interrupt the transport phase by detaching during travel, in contrast with the hitchhiking pathway [13••]. The structure of the different transport networks also influences the direction of dispersal [33,34], leading to a higher propagule pressure in the most connected areas [35•]. The properties of transportation networks, such as their connectedness and the existence of highly connected transportation hubs are potential drivers of bridgehead effects [19]. Finally, the probability of survival of insects during transport depends on factors such as the duration of the transport, exposure to extreme temperatures or limited access to food and water [36••]. These external conditions are more relevant during accidental transport rather than in the harvesting pathway where transport is intentional and designed to keep the species alive. However, in the contamination pathway, insects are often transported with hosts which may provide ideal conditions for surviving transport over long distances.

Arrival phase. Arrival is generally the most studied phase of human-mediated dispersal in insects because the introduction of species into a new location is typically the only phase of human-mediated dispersal easily

Table 1

Characteristics of human activities affecting each phase of human-mediated dispersal in each pathway. Associated references indicate papers that mention the relationship. References with an asterisk correspond to studies on taxa other than insects



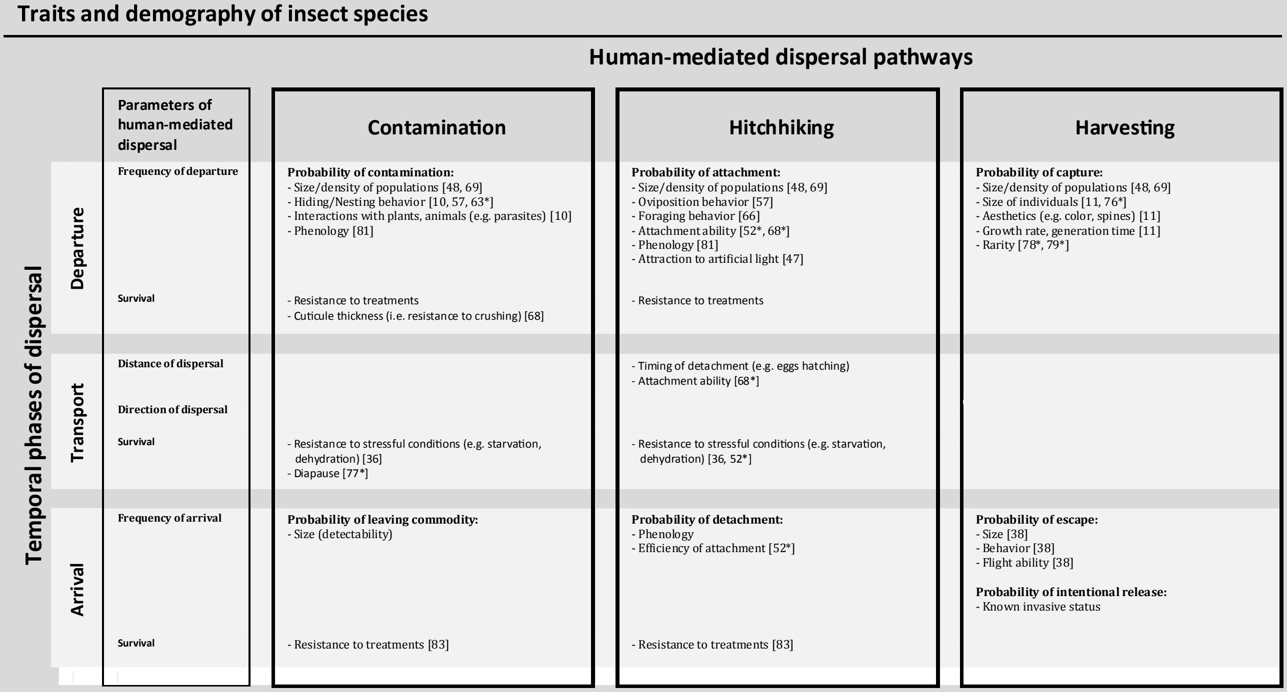
Characteristics of human activities

Human-mediated dispersal pathways

Temporal phases of dispersal	Parameters of human-mediated dispersal	Contamination	Hitchhiking	Harvesting
Departure	Frequency of departure	**Probability of contamination:** - Type of commodity (e.g. soil, plants, wood) [10, 75*] - Amount transported (propagule size) [68] - Frequency of transport (propagule number) [68]	**Probability of attachment:** - Type of vector (e.g. car, boat, train) [13*, 24*, 32] - Number of vectors (i.e. traffic volume) [73*] - Artificial light [47]	**Probability of capture:** - Consumer' demand [71*, 76*] - Harvesting cost - Regulations (e.g. import bans) [72*]
	Survival	- Treatment by exporter [39]	- Treatment by exporter [39]	- Quality of capture (harvesters' experience)
Transport	Distance of dispersal	- Type of human activity (e.g. domestic, industrial) [10, 13*] - Distance traveled by humans [13*, 80]	- Type of human activity (e.g. domestic, industrial) [10, 13*] - Distance traveled by humans [13*]	- Distance between species and costumers [72*]
	Direction of dispersal	- Topology of transportation networks [33, 35, 19] - Human history (e.g. human colonization) [70]	- Topology of transportation networks [33*, 35, 19] - Human history (e.g. human colonization) [70] - Regulations (e.g. import bans) [72*]	- Location of species and customers [72*]
	Survival	- Duration [82] - Temperature range - Oxygen, water and food availability	- Duration - Temperature range - Oxygen, water and food availability	- Quality of transport (e.g. mail, package, service delivery) - Period of the year (i.e. winter in north hemisphere)
Arrival	Frequency of arrival	**Probability of leaving commodity:** - Number of transportation events [66, 73*]	**Probability of detachment:** - Number of vectors (i.e. traffic volume) [73*] - Type of vector - Vibrations	**Probability of escape:** - Quality of containment [11, 38] - Owner experience **Probability of intentional release:** - Type of human activity (e.g. biocontrol, pet trade) [11] - Owner's knowledge about invasion risks - Owner's age - Species' price/ any value
	Survival	- Treatment by importer [39, 74, 75*] - Import control/quarantine [74, 55, 75*] - Proximity to suitable habitats or hosts	-Treatment by importer [39, 74, 75*] - Import control/quarantine [55, 74, 75*] - Proximity to suitable habitats or hosts	- Regulations (e.g. import bans) [74*] - Proximity to suitable habitats or hosts

Table 2

Species traits and demographic parameters can be under selection in each phase of human-mediated dispersal in each pathway. Associated references indicate papers that mention the relationship. References with an asterisk correspond to studies on taxa other than insects



Traits and demography of insect species

Human-mediated dispersal pathways

Temporal phases of dispersal	Parameters of human-mediated dispersal	Contamination	Hitchhiking	Harvesting
Departure	**Frequency of departure**	**Probability of contamination:** - Size/density of populations [48, 69] - Hiding/Nesting behavior [10, 57, 63*] - Interactions with plants, animals (e.g. parasites) [10] - Phenology [81]	**Probability of attachment:** - Size/density of populations [48, 69] - Oviposition behavior [57] - Foraging behavior [66] - Attachment ability [52*, 68*] - Phenology [81] - Attraction to artificial light [47]	**Probability of capture:** - Size/density of populations [48, 69] - Size of individuals [11, 76*] - Aesthetics (e.g. color, spines) [11] - Growth rate, generation time [11] - Rarity [78*, 79*]
	Survival	- Resistance to treatments - Cuticule thickness (i.e. resistance to crushing) [68]	- Resistance to treatments	
Transport	**Distance of dispersal**		- Timing of detachment (e.g. eggs hatching) - Attachment ability [68*]	
	Direction of dispersal			
	Survival	- Resistance to stressful conditions (e.g. starvation, dehydration) [36] - Diapause [77*]	- Resistance to stressful conditions (e.g. starvation, dehydration) [36, 52*]	
Arrival	**Frequency of arrival**	**Probability of leaving commodity:** - Size (detectability)	**Probability of detachment:** - Phenology - Efficiency of attachment [52*]	**Probability of escape:** - Size [38] - Behavior [38] - Flight ability [38] **Probability of intentional release:** - Known invasive status
	Survival	- Resistance to treatments [83]	- Resistance to treatments [83]	

observed [37]. In the harvesting pathway, the quality of containment (e.g. the facilities and boxes in which insects are kept or reared) will influence the probability of escaping captivity [38]. In the two other pathways, quarantine requirements and phytosanitary treatments implemented at ports of entry (e.g. fumigation, cold/heat treatments, irradiation) are often implemented to reduce the insects' probability of surviving the arrival phase [39].

Characteristics of human-mediated dispersal can be modeled to predict the associated risks, and these predictions gain realism when they explicitly consider different parameters involved in each dispersal phase [40,41]. Focusing on the characteristics of human activities could be utilized in generalizable models that can be adapted for a wide range of human activities and various types of insects dispersed by humans through the same pathway [42]. This is important because building a specific human-mediated dispersal model for individual species is both challenging and time-consuming [42].

Species' traits and demography

The different phases of human-mediated dispersal also favor different sets of biological traits. In plants, traits such as large and heavy seeds are favored in the harvesting pathway while the contamination and hitchhiking pathways favor small seed size [43]. Less is known about the traits facilitating transport by insects, though it is clear that species that have historically invaded various world regions are a non-random sample of the global species pools [36••,44,45]. Small sized insects are less likely to be observed and therefore more likely to contaminate material in shipments. For example, small sap-feeding insects are commonly transported with imported live plants [46]. Attraction to light may facilitate association with ships and other transport vectors and thus facilitate transport of insects in the hitchhiking pathway [47].

Departure phase. A high population size and density should increase the probability of being collected accidentally or voluntarily by humans, and thereby increase the frequency of departure [48•,49]. These demographic traits are likely selected for in all three pathways. In the harvesting pathway, insect characteristics such as large body size and fast growth rate increase the probability of being harvested by humans for both the pet trade, and human and pet food [11•]. In the contamination pathway, a strong association with plant species is likely favored, given that plants and parts of plants (e.g. seeds, roots, fruits) are economically important and a frequently transported commodity [46]. This association is the main hypothesis for why Hemiptera and other sap-feeding species are overrepresented among introduced insects [50].

Transport phase. Traits such as higher resistance to stressful conditions such as starvation, dehydration or exposure to toxins during transport are important for surviving the transport phase [36••,51,52]. These traits are likely to be especially favored in the contamination and hitchhiking pathways. Insects that have an extended sessile dormant stage (e.g. diapause or estivation) may be more successfully transported in the hitchhiking pathway. Such traits may not be necessary in the contamination or harvesting pathway as they provide life-sustaining conditions.

Arrival phase. In contamination and hitchhiking pathways, imported commodities and arriving vectors may be subjected to phytosanitary treatments or inspection at ports [53]. Behavior and physiology of some species may make them more resistant to phytosanitary treatments [54]. Small body size (and thus poor detectability) can increase the probability of insects evading detection [46,55]. In the harvesting pathway, small body size, flight abilities or high levels of exploratory behavior might increase the probability of escaping captivity.

The concept that invasions filter species based on their traits is not new [56]. However, studies of differences in traits between native and invasive species (or populations) generally focus on ecological filtering after human-mediated dispersal, that is, during the establishment stage. For example, successful invaders may have a higher competitive ability than native species (or populations) [57–60] or be pre-adapted to new environmental conditions in their introduced range [58,61,62]. Only recently has human-mediated dispersal started to be discussed as an ecological filtering force or selective pressure that might select species or phenotypes based on their propensity to disperse by human activities [13••,36••,63]. Therefore, improving our knowledge on traits favoring species during each dispersal phase is crucial for understanding why some insects are more widely distributed than others [5,64] or for predicting invasion risks of species that may be introduced in the future [40,48•].

Conclusion

In this short review, we do not aim to provide an exhaustive list of factors influencing human-mediated dispersal in insects. Rather, we hope to stimulate further theoretical and experimental research considering phases and pathways as distinct selective filters acting before the establishment and spread of invasive populations. Prevention has been recommended as generally the most efficient approach for managing invasions [65]. Thus, improved knowledge of the drivers of human-mediated dispersal is essential for identifying some of the best options for preventing human activities from dispersing insects at all spatial scales.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Connallon T, Sgrò CM: **In search of a general theory of species' range evolution**. *PLoS Biol* 2018, **16**:1-6.

2. Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J *et al.*: **Grasping at the routes of biological invasions: a framework for integrating pathways into policy**. *J Appl Ecol* 2008, **45**:403-414.

3. Liebhold AM, Tobin PC: **Population ecology of insect invasions and their management**. *Annu Rev Entomol* 2008, **53**:387-408.

4. Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M *et al.*: **No saturation in the accumulation of alien species worldwide**. *Nat Commun* 2017, **8**:1-9.

5. Bertelsmeier C, Ollier S, Liebhold A, Keller L: **Recent human history governs global ant invasion dynamics**. *Nat Ecol Evol* 2017, **1**:1-5.

6. Pagad S, Genovesi P, Carnevali L, Scalera R, Clout M: **IUCN SSC Invasive Species Specialist Group: invasive alien species information management supporting practitioners, policy makers and decision takers**. *Manag Biol Invasions* 2015, **6**:127-135.

7. Bellard C, Cassey P, Blackburn TM: **Alien species as a driver of recent extinctions**. *Biol Lett* 2016, **12**:24-27.

8. Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-massin M, Salles J, Simard F, Courchamp F: **Massive yet grossly underestimated global costs of invasive insects**. *Nature* 2016, **7**:12986.

9. Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG *et al.*: **Nonnative forest insects and pathogens in the United States: impacts and policy options**. *Ecol Appl* 2016, **26**:1437-1455.

10. • Meurisse N, Rassati D, Hurley BP, Brockerhoff EG, Haack RA: **Common pathways by which non-native forest insects move internationally and domestically**. *J Pest Sci* 2019, **92**:13-27.

A review of unintentional human-mediated dispersal of non-native forest insects. The authors describe the human-mediated dispersal pathways responsible for the international and regional spread of insects. They also illustrate the non-random relative frequencies of insect orders among different dispersal pathways.

11. • Kumschick S, Devenish A, Kenis M, Rabitsch W, Richardson DM, Wilson JRU: **Intentionally introduced terrestrial invertebrates: patterns, risks, and options for management**. *Biol Invasions* 2016, **18**:1077-1088.

A review of the intentional dispersal of insects. This paper lists the diverse, yet understudied, reasons for the intentional transport of invertebrates. The authors also address the traits that favour a species' selection, and consequent transport, for the different types of human activities identified.

12. Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ *et al.*: **Invasion science: a horizon scan of emerging challenges and opportunities**. *Trends Ecol Evol* 2017, **32**:464-474.

13. •• Bullock JM, Bonte D, Pufal G, da Silva Carvalho C, Chapman DS, García C, García D, Matthysen E, Delgado MM: **Human-mediated dispersal and the rewiring of spatial networks**. *Trends Ecol Evol* 2018, **33**:958-970.

A general review emphasizing the importance of human-mediated dispersal in biological invasions. The authors discuss the importance of considering how human activities influence species spread and filter species based on their traits. They also point the utility of decomposing human-mediated dispersal into temporal phases in order to better understand this process.

14. Gotzek D, Axen HJ, Suarez AV, Helms Cahan S, Shoemaker D: **Global invasion history of the tropical fire ant: a stowaway on the first global trade routes**. *Mol Ecol* 2015, **24**:374-388.

15. Lesieur V, Lombaert E, Guillemaud T, Courtial B, Strong W, Roques A, Auger-Rozenberg M: **The rapid spread of *Leptoglossus occidentalis* in Europe: a bridgehead invasion**. *J Pest Sci* 2019, **92**:189-200.

16. Garnas JR, Auger-Rozenberg MA, Roques A, Bertelsmeier C, Wingfield MJ, Saccaggi DL, Roy HE, Slippers B: **Complex patterns of global spread in invasive insects: eco-evolutionary and management consequences**. *Biol Invasions* 2016, **18**:935-952.

17. • Bertelsmeier C, Ollier S, Liebhold AM, Brockerhoff EG, Ward D, Keller L: **Recurrent bridgehead effects accelerate global alien ant spread**. *Proc Natl Acad Sci U S A* 2018, **115**:5486-5491.

This paper highlights the importance of established invasive populations as a source of new invasions. Using long-term data on ant interceptions at air and maritime ports, they find that most ant introductions occur via an intermediate region, demonstrating a positive feedback loop between the introduction and establishment phases of the invasion process.

18. Javal M, Lombaert E, Tsykun T, Courtin C, Kerdelhué C, Prospero S, Roques A, Roux G: **Deciphering the worldwide invasion of the Asian long-horned beetle: a recurrent invasion process from the native area together with a bridgehead effect**. *Mol Ecol* 2019, **28**:951-967.

19. Bertelsmeier C, Keller L: **Bridgehead effects and role of adaptive evolution in invasive populations**. *Trends Ecol Evol* 2018, **33**:527-534.

20. Sharma GP, Esler KJ, Blignaut JN: **Determining the relationship between invasive alien species density and a country's socio-economic status**. *S Afr J Sci* 2010, **106**:1-7.

21. Essl F, Dullinger S, Rabitsch W, Hulme PE, Hulber K, Jarosik V, Kleinbauer I, Krausmann F, Kuhn I, Nentwig W *et al.*: **Socioeconomic legacy yields an invasion debt**. *Proc Natl Acad Sci U S A* 2011, **108**:203-207.

22. Gallardo B, Zieritz A, Aldridge DC: **The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders**. *PLoS One* 2015, **10**:1-17.

23. Capinha C, Essl F, Seebens H, Pereira HM, Kühn I: **Models of alien species richness show moderate predictive accuracy and poor transferability**. *NeoBiota* 2018, **38**:77-96.

24. Auffret AG, Berg J, Cousins SAO: **The geography of human-mediated dispersal**. *Divers Distrib* 2014, **20**:1450-1456.

25. Bowler DE, Benton TG: **Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics**. *Biol Rev* 2005, **80**:205-225.

26. Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M *et al.*: **Costs of dispersal**. *Biol Rev* 2012, **87**:290-312.

27. Pergl J, Pyšek P, Bacher S, Essl F, Genovesi P, Harrower CA, Hulme PE, Jeschke JE, Kenis M, Kühn I *et al.*: **Troubling travellers: are ecologically harmful alien species associated with particular introduction pathways?** *NeoBiota* 2017, **32**:1-20.

28. King JR, Tschinkel WR, Ross KG: **A case study of human exacerbation of the invasive species problem: transport and establishment of polygyne fire ants in Tallahassee, Florida, USA**. *Biol Invasions* 2008, **11**:373-377.

29. McFadden MW, McManus ME: **An insect out of control? The potential for spread and establishment of the gypsy moth in new forest areas in the United States**. In *Forest Insect Guilds: Patterns of Interaction with Host Trees.* Edited by Baranchikov YN, Mattson WJ, Hain FP, Payne TL. 1991:172-186. USDA For. Serv. Gen. Tech. Rep. NE 153.

30. Inari N, Nagamitsu T, Kenta T, Goka K, Hiura T: **Spatial and temporal pattern of introduced *Bombus terrestris* abundance in Hokkaido, Japan, and its potential impact on native bumblebees**. *Popul Ecol* 2005, **47**:77-82.

31. Simberloff D: **The role of propagule pressure in biological invasions**. *Annu Rev Ecol Syst* 2009, **40**:81-102.

32. • Eritja R, Palmer JRB, Roiz D, Sanpera-Calbet I, Bartumeus F: **Direct evidence of adult *Aedes albopictus* dispersal by car**. *Sci Rep* 2017, **7**:14399.

The authors use a sampling study to verify the transport of adult tiger mosquitos (*Aedes albopictus*) in cars, and estimate the frequency of transport events. In combination with citizen science data on mosquito prevalence, they use a Bayesian model incorporating commuting patterns to model inter-regional flows of tiger mosquitoes in Spain and identify key transport hubs.

33. Banks NC, Paini DR, Bayliss KL, Hodda M: **The role of global trade and transport network topology in the human-mediated dispersal of alien species**. *Ecol Lett* 2015, **18**:188-199.

34. Chapman D, Purse BV, Roy HE, Bullock JM: **Global trade networks determine the distribution of invasive non-native species**. *Glob Ecol Biogeogr* 2017, **26**:907-917.

35. • Morel-Journel T, Assa CR, Mailleret L, Vercken E: **It's all about connections: hubs and invasion in habitat networks**. *Ecol Lett* 2018, **22**:313-321.

This paper demonstrates the importance of connectivity and species demography for spread dynamics in a dispersal network, by coupling computer simulations and microcosms experiments to reproduce invasions by the parasitoid wasp *Trichogramma chilonis.*

36. •• Renault D, Laparie M, McCauley SJ, Bonte D: **Environmental adaptations, ecological filtering, and dispersal central to insect invasions**. *Annu Rev Entomol* 2018, **63**:345-368.

A general review addressing the importance of environmental filtering throughout the invasion process. The authors focused their analysis on the role of dispersal abilities and stress resistance in invasion success, and raise questions about how the potential interactions between these two selective forces could either enhance spread dynamics or lead to trade-offs between a species ability for natural dispersal or for dispersal with humans.

37. Puth LM, Post DM: **Studying invasion: have we missed the boat?** *Ecol Lett* 2005, **8**:715-721.

38. American Committee of Medical Entomology: **American society of tropical medicine and hygiene: arthropod containment guidelines, version 3.2**. *Vector Borne Zoonotic Dis* 2019, **19**:152-173.

39. Allen E, Noseworthy M, Ormsby M: **Phytosanitary measures to reduce the movement of forest pests with the international trade of wood products**. *Biol invasions* 2017, **19**:3365-3376.

40. Cope RC, Ross JV, Wittmann TA, Watts MJ, Cassey P: **Predicting the risk of biological invasions using environmental similarity and transport network connectedness**. *Risk Anal* 2019, **39**:35-53.

41. Lustig A, James A, Anderson D, Plank M: **Pest control at a regional scale: identifying key criteria using a spatially explicit, agent-based model**. *J Appl Ecol* 2019, **56**:1515-1527.

42. Savage D, Renton M: **Requirements, design and implementation of a general model of biological invasion**. *Ecol Modell* 2014, **272**:394-409.

43. von der Lippe M, Kowarik I: **Interactions between propagule pressure and seed traits shape human-mediated seed dispersal along roads**. *Perspect Plant Ecol Evol Syst* 2012, **14**:123-130.

44. Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B: **Increasing numbers and intercontinental spread of invasive insects on eucalypts**. *Biol Invasions* 2016, **18**:921-933.

45. Liebhold AM, Yamanaka T, Roques A, Augustin S, Chown SL: **Global compositional variation among native and non-native regional insect assemblages emphasizes the importance of pathways**. *Biol Invasions* 2016, **18**:893-905.

46. Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO: **Live plant imports: the major pathway for forest insect and pathogen invasions of the US**. *Front Ecol Environ* 2012, **10**:135-143.

47. Wallner WE, Humble LM, Levin RE, Baranchikov YN, Carde RT: **Response of adult lymantriid moths to illumination devices in the Russian Far East**. *J Econ Entomol* 1995, **88**:337-342.

48. • Liebhold AM, Brockerhoff EG, Kimberley M: **Depletion of heterogeneous source species pools predicts future invasion rates**. *J Appl Ecol* 2017, **54**:1968-1977.

Using a mechanistic model of bark beetle (Scolytinae) invasions, the authors find that despite the depletion of species source pools, the establishment of new species is likely to continue due to increased import rates. The paper demonstrates that the understanding of key underlying mechanisms in the invasion process is crucial for predicting future invasions.

49. Guo WY, Essl F, Weigelt P, Van Kleunen M, Pyšek P, Pierce S, Dawson W, Kreft H, Maurel N, Pergl J: **Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization**. *Glob Ecol Biogeogr* 2019, **28**:628-639.
50. Yamanaka T, Morimoto N, Nishida GM, Kiritani K, Moriya S, Liebhold AM: **Comparison of insect invasions in North America, Japan and their Islands**. *Biol Invasions* 2015, **17**:3049-3061.
51. Villena OC, Terry I, Iwata K, Landa ER, LaDeau SL, Leisnham PT: **Effects of tire leachate on the invasive mosquito Aedes albopictus and the native congener *Aedes triseriatus***. *PeerJ* 2017, **5**:e3756.
52. Collas FPL, Karatayev AY, Burlakova LE, Leuven RSEW: **Detachment rates of dreissenid mussels after boat hull-mediated overland dispersal**. *Hydrobiologia* 2018, **810**:77-84.
53. Whattam M, Clover G, Firko M, Kalaris T: **The biosecurity continuum and trade: border operations**. In *The Handbook of Plant Biosecurity.* Edited by Gordh G, McKirdy S. Dordrecht: Springer; 2014:149-188.
54. Schortemeyer M, Thomas K, Haack RA, Uzunovic A, Hoover K, Simpson JA, Grgurinovic CA: **Appropriateness of probit-9 in the development of quarantine treatments for timber and timber commodities**. *J Econ Entomol* 2011, **104**:717-731.
55. Eschen R, Rigaux L, Sukovata L, Vettraino AM, Marzano M, Grégoire JC: **Phytosanitary inspection of woody plants for planting at European Union entry points: a practical enquiry**. *Biol invasions* 2015, **17**:2403-2413.
56. Holway DA, Suarez AV: **Animal behavior: an essential component of invasion biology**. *Trends Ecol Evol* 1999, **14**:328-330.
57. Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ: **The causes and consequences of ant invasions**. *Annu Rev Ecol Syst* 2002, **33**:181-233.
58. Wills BD, Moreau CS, Wray BD, Hoffmann BD, Suarez AV: **Body size variation and caste ratios in geographically distinct populations of the invasive big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae)**. *Biol J Linn Soc* 2014, **113**:423-438.
59. Blight O, Josens R, Bertelsmeier C, Abril S, Boulay R, Cerdá X: **Differences in behavioural traits among native and introduced colonies of an invasive ant**. *Biol Invasions* 2017, **19**:1389-1398.
60. Felden A, Paris CI, Chapple DG, Haywood J, Suarez AV, Tsutsui ND, Lester PJ, Gruber MAM, Zealand N: **Behavioural variation and plasticity along an invasive ant introduction pathway**. *J Anim Ecol* 2018, **87**:1653-1666.
61. Foucaud J, Rey O, Robert S, Crespin L, Orivel J, Facon B, Loiseau A, Jourdan H, Kenne M, Masse PSM *et al.*: **Thermotolerance adaptation to human-modified habitats occurs in the native range of the invasive ant *Wasmannia auropunctata* before long-distance dispersal**. *Evol Appl* 2013, **6**:721-734.
62. Jarošík V, Kenis M, Honêk A, Skuhrovec J, Pyšek P: **Invasive insects differ from non-invasive in their thermal requirements**. *PLoS One* 2015, **10**:e0131072.

Further reading

63. Chapple DG, Simmonds SM, Wong BBM: **Can behavioral and personality traits influence the success of unintentional species introductions?** *Trends Ecol Evol* 2012, **27**:57-64.
64. Roques A, Auger-Rozenberg MA, Blackburn TM, Garnas J, Pyšek P, Rabitsch W, Richardson DM, Wingfield MJ, Liebhold AM, Duncan RP: **Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years**. *Biol Invasions* 2016, **18**:907-920.
65. Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G: **An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species**. *Proc R Soc B Biol Sci* 2012, **269**:2407-2413.
66. Egizi A, Kiser J, Abadam C, Fonseca DM: **The hitchhiker's guide to becoming invasive: Exotic mosquitoes spread across a US state by human transport not autonomous flight**. *Mol Ecol* 2016, **25**:3033-3047.
67. Mikheyev AS, Tchingnoumba L, Henderson A, Alonso A, Mikheyev AS, Tchingnoumba L, Henderson A: **Effect of propagule pressure on the establishment and spread of the little fire ant *Wasmannia auropunctata* in a gabonese oilfield**. *Divers Distrib* 2008, **14**:301-306.
68. Bacela-Spychalska K: **Attachment ability of two invasive amphipod species may promote their spread by overland transport**. *Aquat Conserv Mar Freshw Ecosyst* 2016, **26**:196-201.
69. Morrison A, Sweeney J, Hughes C, Johns RC: **Hitching a ride: firewood as a potential pathway for range expansion of an exotic beech leaf-mining weevil, *Orchestes fagi* (Coleoptera: Curculionidae)**. *Can Entomol* 2017, **137**:129-137.
70. Panagiotakopulu E, Buckland PC: **A thousand bites – insect introductions and late Holocene environments**. *Quat Sci Rev* 2017, **156**:23-35.
71. Nijman V, Nekaris KA: **The Harry Potter effect: the rise in trade of owls as pets in Java and Bali, Indonesia**. *Glob Ecol Conserv* 2017, **11**:84-94.
72. Reino L, Figueira R, Beja P, Araújo MB, Capinha C, Strubbe D: **Networks of global bird invasion altered by regional trade ban**. *Sci Adv* 2017, **3**:e1700783.
73. Tatem AJ, Hay SI, Rogers DJ: **Global traffic and disease vector dispersal**. *Proc Natl Acad Sci U S A* 2006, **103**:6242-6247.
74. Poland TM, Rassati D: **Improved biosecurity surveillance of non-native forest insects: a review of current methods**. *J Pest Sci* 2019, **92**:37-49.
75. Sikes BA, Bufford JL, Hulme PE, Cooper JA, Johnston R, Duncan RP: **Import volumes and biosecurity interventions shape the arrival rate of fungal pathogens**. *PLoS Biol* 2018, **16**:e2006025.
76. Zeng Y, Yan K, Erin C, Lodge DM, Yeo DCJ: **Disregarding human pre-introduction selection can confound invasive crayfish risk assessments**. *Biol Invasions* 2015, **17**:2373-2385.
77. Panov VE, Caceres C: **Role of diapause in dispersal of aquatic invertebrates**. In *Diapause in Aquatic Invertebrates.* Edited by Alekseev V, De Stasio B, Gilbert JJ. Dordrecht: Springer; 2007:187-195.
78. Courchamp F, Angulo E, Rivalan P, Hall RJ, Signoret L, Bull L, Meinard Y: **Rarity value and species extinction: the anthropogenic Allee effect**. *PLoS Biol* 2006, **4**:2405-2410.
79. Angulo E, Deves AL, Saint Jalmes M, Courchamp F: **Fatal attraction: rare species in the spotlight**. *Proc R Soc B Biol Sci* 2009, **276**:1331-1337.
80. Koch FH, Yemshanov D, Magarey RD, Smith WD: **Dispersal of invasive forest insects via recreational firewood: a quantitative analysis**. *J Econ Entomol* 2012, **105**:438-450.
81. Carrasco LR, Mumford JD, MacLeod A, Harwood T, Grabenweger G, Leach AW, Knight JD, Baker RHA: **Unveiling human-assisted dispersal mechanisms in invasive alien insects: integration of spatial stochastic simulation and phenology models**. *Ecol Modell* 2010, **221**:2068-2075.
82. Fick WE, MacQuarrie CJK: **An artificial delay in emergence influences the number but not the fitness of adult emerald ash borer emerging from infested ash wood**. *Entomol Exp Appl* 2018, **166**:171-182.
83. Roberts PB, Follett PA: **Food irradiation for phytosanitary and quarantine treatment**. In *Food Irradiation Technologies – Applications for Preservation.* Edited by Ferreira LCFR, Antonio AL, Cabo Verde SC. Cambridge, UK: Royal Society of Chemistry; 2017:169-182.